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# SEXUAL DIMORPHISM IN EYE MORPHOLOGY IN *EUCHEIRA SOCIALIS* (PIERIDAE)

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**ABSTRACT.** We examined the magnitude of sexual dimorphism in the eyes of madrone butterflies, *Eucheira socialis* (Pieridae). Via microscopic examination of the cornea, we determined the eye surface area, facet number, and facet diameter in 5 eye regions for males and females. Our analysis, which controlled for body size (forewing length), showed that in this species, as in most Lepidoptera, males have a significantly larger eye surface area and more facets than females. Facet diameters vary with eye region but in an unusual way for the Lepidoptera: the largest facets we observed were in the dorsal region of the male eye. While the results reveal interesting patterns of sexual dimorphism in eye structure in *E. socialis* there is insufficient information about adult behavior to understand the behavioral and ecological implications and causes of these patterns, especially those in facet diameter.

**Additional key words:** sexual dimorphism, eye structure, eye size, facet diameter.

Sexual dimorphism in eye structure is common in the Lepidoptera (Yagi & Koyama 1963). Males usually have eyes that are larger and have more and larger facets than those of females. In response to a presentation on sexual dimorphism in butterfly eyes by one of us (RLR) at the 1999 meeting of the Lepidopterists' Society, Dr. Arthur Shapiro suggested that sexual dimorphism in eye structure was particularly pronounced in the madrone butterfly, *Eucheira socialis* Westwood (Pieridae). We investigated this claim by examining corneal structure in males and females of this species.

Little has been reported about the behavior of *E. socialis* adults that bears on the question of selection pressures that might have shaped eye structure. Previous studies of *E. socialis* have focused on the social behavior of the larvae and the relationship between this butterfly and madrone trees (*Arbutus* spp., Ericaceae) on which the larvae feed (Kevan & Bye 1991, Underwood 1992, 1994). The adults live for approximately one week and are apparently unable to feed because the two halves of the proboscis do not anneal correctly. Within 3 h of eclosion adult females generally travel about 15–18 m to oviposit. A female lays her eggs in a single large mass (20 to over 350 eggs) on the ventral side of one madrone leaf (Underwood 1992). Males fly around madrones and other trees in the vicinity only when there is bright sunlight (D. Underwood pers. comm.). The mating behavior of males and females is essentially unknown.

## Materials and Methods

The *E. socialis* specimens used in this study were obtained from Art Shapiro (University of California, Davis) and Dessie Underwood (California State University, Long Beach) and reported to have been reared in April 1991 from larvae found in two nests in the Sierra Madre Occidental, Durango, Mexico. We received them as papered specimens. We processed each of 5 males and 5 females in the following way. We measured the forewing length (FWL) to the nearest 0.1 mm using dial calipers. Then the head was removed, bisected, and immersed in 10% NaOH solution until the soft tissue could be gently removed from each cornea, approximately 5 minutes. Non-corneal cuticle was trimmed away from the eye. Radial cuts—two starting close together dorsally, one starting ventrally, and some starting both anteriorly and posteriorly from the edges of the cornea—were made toward the center of the cornea (Fig. 1). These permitted the cornea to lie flat on a microscope slide and provided references for identification of eye regions. To improve the visibility of the cornea for handling, we applied acid fuchsia stain for a few minutes to the cornea. Finally, the cornea was mounted in glycerol and covered with a coverslip, the edges of which we sealed with Cytosol 60 mounting medium (Stephen Scientific).

Digitized images of each cornea were obtained by video microscopy with a Nikon inverted microscope. Approximately 15 images of each cornea made with a 10× objective were required to capture the entire cornea. A composite image of each complete cornea (for example, see Fig. 1) was created using Adobe Photoshop (Adobe Systems Incorporated). For a size reference a micrometer scale at 10× was photographed.

The numbers of facets in the cornea were manually counted from the composite images. However, we used image analysis software (Scion Image) to measure facet diameters and eye surface area (ESA) from the composite images. The micrometer scale on each image was used to calibrate the software. To obtain the ESA of each image an outline tool was used. Two ESA measurements taken by this method were averaged to control for error in tracing the image; if the two measurements differed by more than 5%, then a third measurement was included in the average. Facet di-

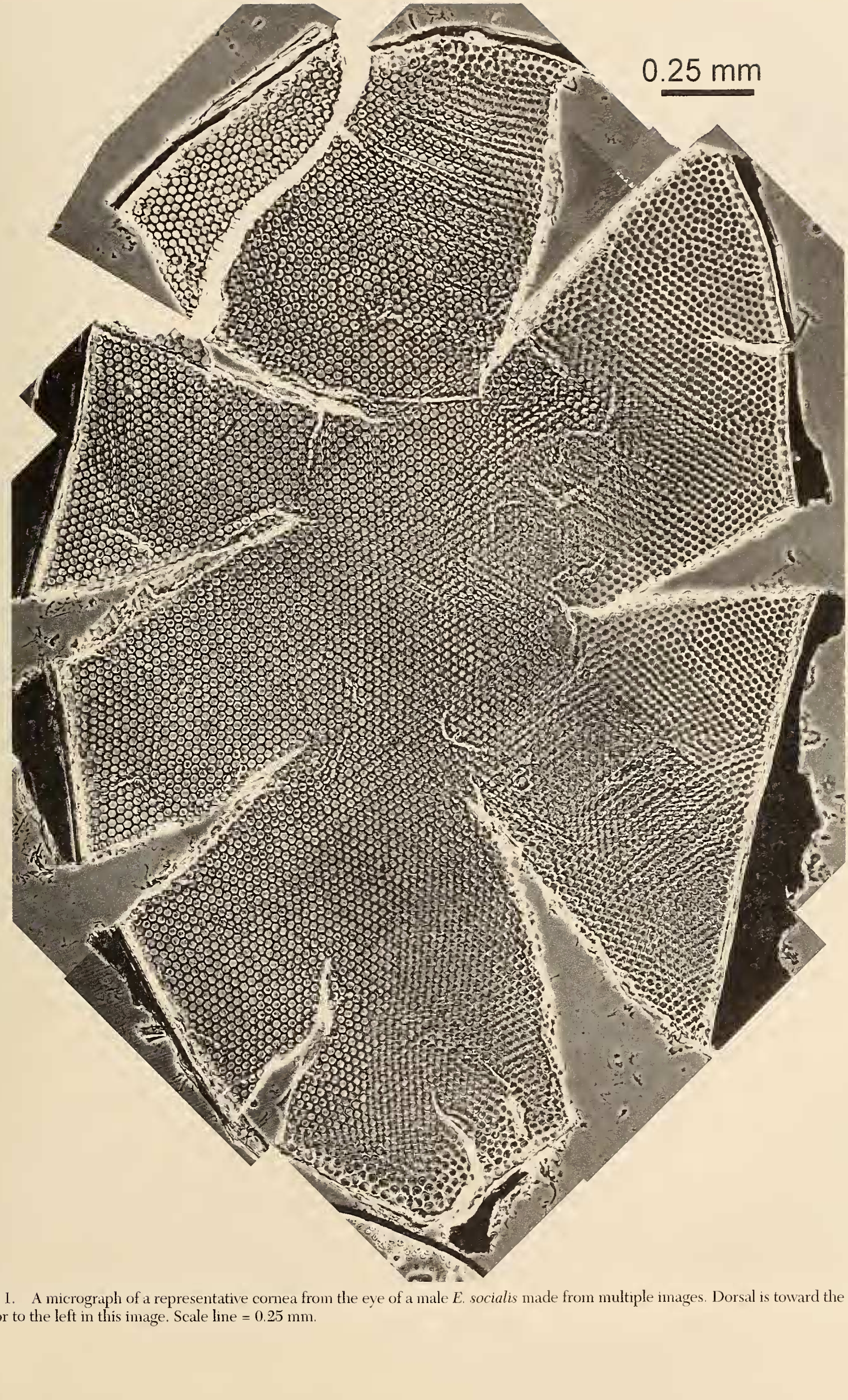


FIG. 1. A micrograph of a representative cornea from the eye of a male *E. socialis* made from multiple images. Dorsal is toward the top and anterior to the left in this image. Scale line = 0.25 mm.

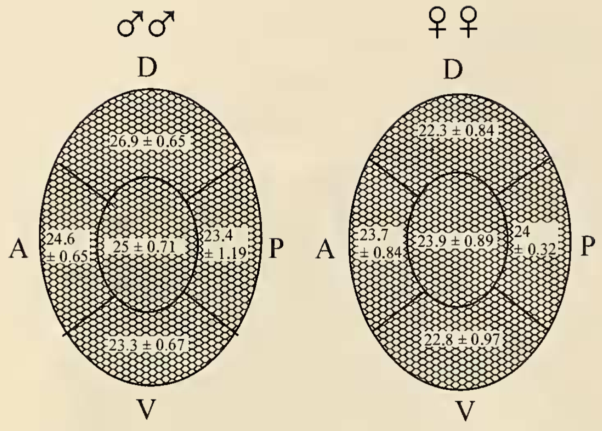


FIG. 2. Schematic of the cornea of *E. socialis* showing the facet diameters (in mm; mean ± standard deviation) measured for both males and females in each of five regions of the cornea. Abbreviations: A, anterior; D, dorsal; P, posterior; V, ventral.

ameters were calculated by dividing the length of a row of 10 facets by 10. Two measurements were taken in each of the 5 eye regions (anterior, posterior, dorsal, ventral, center), then averaged. If the two measurements differed by more than 8%, then a third measurement was included in the average. The measurement points within each eye region were chosen based on the clarity of the facet images within that region (i.e. no wrinkles or tears in the cornea). All statistical analyses were done on SYSTAT 9.0 (SYSTAT, Inc.).

## RESULTS

The males in our sample were significantly smaller than the females as measured by forewing length (males: 25.7 ± 1.22 mm; females: 31.2 ± 1.43 mm; $t$ = 6.58, 8 df, $p < 0.0002$). Despite their smaller body size, males have a significantly larger ESA than females (males: 4.45 ± 0.15 $mm^2$; females: 3.20 ± 0.15 $mm^2$; ANCOVA, with forewing length as covariate, $p < 0.0001$). ESA is not correlated with forewing length within either sex ($p = 0.135$), although sample sizes were small.

A larger ESA in males could mean that compared to females they have more facets, larger facets, or both. Males have significantly more facets (7781 ± 85) than females (6648 ± 357: ANCOVA, with forewing length as covariate, $p = 0.011$), but within the sexes there was no significant correlation between facet number and ESA ($p = 0.117$).

The mean facet diameters for each of the five eye regions in males and females are illustrated in Fig. 2. A two-way repeated measures ANOVA with facet diameter as the dependent variable and region as the repeated measure showed that the effects of region, sex, and the interaction between sex and eye region were all significant ($p < 0.001$ for each). Therefore, variation in facet diameters is explained by both sex and eye region, but there are significant differences between sexes in the pattern of variation among regions. Facet diameters of males were generally larger than those of females but especially in the dorsal region. In fact, only in the dorsal eye region was the difference in facet diameter between males and females significant ($t$ = 8.69, 8 df, $p < 0.0001$). Facet diameters did not differ significantly between males and females in any other eye regions (anterior, $t$ = 1.9, posterior, $t$ = 0.368, ventral, $t$ = 0.376; center, $t$ = 2.157; all: 8 df, $p > 0.05$). Another clear trend in the eyes of both males and females was that facets in the ventral region tended to be smaller than those in the anterior, central, and posterior regions along the equator of the eye.

## DISCUSSION

Compared with conspecific females who are on average larger in body size, *E. socialis* males have eyes that are 1.39 times larger in surface area, have 1.17 times more facets, and have, at least dorsally, larger facet lenses. Contrary to Dr. Shapiro's initial impression, this sexual dimorphism in eye morphology is similar in direction and magnitude to that seen in butterflies and other Lepidoptera (Rutowski 2000). For comparison, Yagi and Koyama (1963) report male : female eye surface area ratios of 1.37 and 1.33 and facet number ratios of 1.1 and 1.18 for two pierids, *Colias erate* and *Pieris rapae*, respectively. Eyes in males that are larger and have more ommatidia relative to body size than those in females are generally interpreted as indicating that acute vision in males is more important to reproductive success than in females (Rutowski 2000, and in press).

In spite of this general similarity in eye structure, the pattern of variation in facet diameters is quite different from that reported for another butterfly, *Asterocampa leilia*. In *A. leilia* the largest facets are found in the frontal and dorsofrontal regions of the eye regions with facets in the dorsal region being smaller (Ziemba & Rutowski 2000). Large facets indicate eye regions of high resolution and sensitivity and imply that those regions of the eye are frequently used in specific tasks requiring high resolution or sensitivity such as when males track females during rapid pursuit flights (Land 1989, 1997). The large facets in the dorsal part of the male eye in *E. socialis* suggest that dorsal vision is better than in other parts of the visual field. Little is known about the behavior of adult madrone butterflies so the possible functions of this dorsal region of high acuity are not clear, but it might be important in sexual interactions. In some insects, acute dorsal vision produced by large facets is important in males for detecting females against the sky (Land 1997). Some pierids have been observed engaging in ascending flights during courtship attempts. During an ascending flight a male-female pair flies up together until one of them, usually the male, terminates pursuit and drops rapidly toward the ground (Rutowski 1978a, b). When Dessie Underwood threw *E. socialis* females up in the air in an attempt to pair them, she noted that *E. socialis* males would only chase the female if she flew well (D. Underwood pers. com.). If ascending flights are a common occurrence in *E. socialis* courtship, then the male's dorsal acute zone may be used for tracking the female's movements in this context.

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